NON-MONOPHYLY OF AUCHENORRHYNCHA ("HOMOPTERA"), BASED UPON 18S rDNA PHYLOGENY: ECO-EVOLUTIONARY AND CLADISTIC IMPLICATIONS WITHIN PRE-HETEROPTERODEA HEMIPTERA (S.L.) AND A PROPOSAL FOR NEW MONOPHYLETIC SUBORDERS

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Abstract.—Parsimony-based phylogenetic analyses of full 18S rRNA genes (18S rDNA) were conducted to determine the basal clade topology of Hemiptera. The single most parsimonious topology, which attenuated homoplasy and retained only the most conservative base sites, showed: (a) Sternorrhyncha and Euhemiptera are sister-clades; (b) Cicadomorpha (composed of Cicadidae and sister-clade Cercopidae+Membracidae) is sister-clade to the remaining Euhemiptera; and (c) Fulgoromorpha is sister-clade to Heteropterodea (Coleorhyncha+Heteroptera). Supportive morphological synapomorphies for the 18S rDNA topology are listed. Less parsimonious, but competitive topologies indicate association of Heteroptera with extant Cicadomorpha. Thus, Auchenorrhyncha is unlikely (< 10%) to be monophyletic, as previously assumed, and its morphological synapomorphies (tymbal acoustic systems, aristoid antennae, ScP+R vein fusion) are homoplasious; the misinterpretation, selection, and convergence of these traits is discussed. Current paleontological assessments of the basal Hemiptera are reviewed and also suggest non-monophyly for Auchenorrhyncha. A Lower Cretaceous fossil, *Megaleurodes megocellata* Hamilton, previously assigned to Aleyrodoidea: Boreoscytidae, is tentatively reassigned to fossil superfamily Fulgoridioidea of Fulgoromorpha. Use of paraphyletic Auchenorrhyncha should be abandoned as a hemipteran suborder; instead recognition of the four monophyletic basal clades of Hemiptera as its suborders is appropriate. Three new suborder names are proposed because of potential confusions or varying definitions (discussed) involving existing names: Clypeorrhyncha (= extant, monophyletic Cicadomorpha), Archaeorrhyncha (= Fulgoromorpha), and Prosorrhyncha (= Heteropterodea, as clade Coleorhyncha+Heteroptera); Sternorrhyncha is retained. Clade name Neohemiptera is proposed for the clade Fulgoromorpha+Heteropterodea. An eco-evolutionary scenario for cladogenesis among the basal hemipteran clades is presented. Evidence indicates a saltational, punctuated equilibrium mode of evolution occurred among the clades during, or near, the Permian.

Key Words.—Insecta, Cicadomorpha, Fulgoromorpha, molecular phylogeny, cladistics

The hierarchical, ordinal relationship among the names "Hemiptera," "Heteroptera," and "Homoptera" has been confused since Latreille (1810) first recognized the latter two names as sections of his "Hemiptera" (sensu lato). This was done in response to Fabricius' (1775) mouthpart-based modification of Linnaeus' (1758) original wing-based classification of insect orders; see Henry & Froeschner (1988: xii–xiii) for discussion. Current schemes for recognition of (an) order(s) for all hemipterans differ confusingly among workers and regions. Some prefer the separate orders Homoptera and Hemiptera (sensu strictu, sensu La-

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treille's Heteroptera), following the revisions of Borror & DeLong's (e.g., 1971) books. Others use order Hemiptera (s.l., sensu Latreille) with suborders Homoptera and Heteroptera. Still others use the separate orders Homoptera and Heteroptera.

Although sometimes presenting operational problems for a classification (Sorensen 1990: 402), application of monophyly through cladistic philosophy is being used to solve the dilemma of hierarchical grouping in Heteroptera (Schuh 1986), and hopefully for all hemipterans here. On the basis of morphology, cladistic workers (Kristensen 1975, 1991; Hennig 1981; Popov 1981; Schuh 1979; Wootton & Betts 1986) now recognize that Homoptera is a paraphyletic grade at the base of monophyletic Heteroptera, with the entire greater clade usually recognized as Hemiptera. Accordingly, order Homoptera must be abandoned under a monophyly criterion, despite the resistance of many homopterists to having their groups incorporated into Hemiptera because they associate that name with a usage now replaced by Heteroptera (e.g., Henry & Froeschner 1988).

Recent treatments (e.g., Carver et al. 1991: 443) of Hemiptera retain Sternorrhyncha and Auchenorrhyncha as hemipteran suborders, based on their respective *assumed* monophyly[4]. Sternorrhyncha is now considered a sister-group (Schuh 1979, Carver et al. 1991, Wheeler et al. 1993) to Auchenorrhyncha + Heteroptera[5] (= Euhemiptera sensu Schuh 1979). Now, Campbell et al. (1994) show irrefutable evidence of the monophyly of Sternorrhyncha, as a synapomorphy having a unique nucleotide expansion area of 18S rDNA. Thus, Sternorrhyncha is a cladistically valid hemipteran suborder. In Campbell et al.'s (1994) analysis, however, Auchenorrhyncha was paraphyletic, a result that is cladistically incompatible with its use as a hemipteran suborder.

Wheeler et al. (1993) used discontinuous, short sections of 18S rDNA and morphological data, alone and in combination, in a parsimony analysis to show in their most resolute indications that their "Auchenorrhyncha" were a monophyletic grouping. However, because that analysis was chiefly concerned with relationships within Heteroptera, it included only minimal representatives of Cicadomorpha[6] (sensu Carver et al. 1991, and here), and showed their monophyly to be based upon two 18S rDNA sites that were homoplasious when considered over their entire generated tree. Unfortunately, they excluded Fulgoromorpha, the putative sister-group to Cicadomorpha (Carver et al. 1991: 445). As a consequence, Wheeler et al.'s (1993) analysis established only: (a) tentative monophyly, based upon nucleotide homoplasy under parasimony, for their treated cicadomorphans rather than among all auchenorrhynchous groups; and (b) that (in the absence of Fulgoromorpha) their cicadomorphan taxa (≠ Cercopidae, Membracidae) formed a sister-group to Heteropterodea, the latter as clade Coleorhyncha + Heteroptera (sensu Schlee 1969, Schuh 1979).

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[4] Hamilton (1981) considered Auchenorrhyncha to be polyphyletic, based on head morphology, with its groups surrounding his "Aphidomorpha" (= Sternorrhyncha); however, he considered the Homoptera, itself, to be monophyletic and the sister-group of Heteropterodea (sensu Schuh 1979).

[5] Carver et al. (1991) use Heteroptera [sensu lato] to include Coleorhyncha + Heteroptera [sensu stricto: e.g., Henry & Froeschner (1988)], a clade considered Heteropterodea (Schuh 1979) [= Heteropteroidea (Schlee 1969)] here.

[6] Wheeler et al. (1993) used a single Cicadidae [*Tibicen* sp.] and two Cicadellidae [*Graphocephala coccinea* (Forster), *Oncometopia orbona* (Fabr.)] species.

In contrast, Campbell et al.'s (1994) analysis included exemplar taxa from Fulgoromorpha (Flatidae), Cicadomorpha (Cercopidae, Cicadidae, Membracidae), Sternorrhyncha (Psyllidae, Aphididae, Diaspididae, Aleyrodidae) and Heteroptera (Miridae). They mention, but do not discuss, the paraphyly of Auchenorrhyncha because that study's purpose was only to establish monophyly for Sternorrhyncha and its internal phylogeny with reference to the derivation of Aleyrodidae.

This article: (a) analyzes an expanded set of the 18S rDNA nucleotide sequences used by Campbell et al. (1994) and derives the basal phylogenetic topology among major clades of hemipterans; (b) discusses the morphological characters previously assumed to be valid synapomorphies for Auchenorrhyncha, but that must represent homoplasies according to our 18S rDNA analyses; (c) lists supporting morphological synapomorphies for the 18S rDNA-based tree; (d) discusses the eco-evolutionary scenario involved with cladogenesis of the 18S rDNA-based tree; and (e) proposes cladistically compatible category names to reflect the realignment of the basal phylogeny of Hemiptera.

DISCUSSION OF METHODS

Chemically-Based Procedures.—Preparation followed Campbell et al. (1994). Total genomic DNA was purified by homogenizing fresh insects, or parts thereof, in micro-centrifuge tubes with a pestle in 200 μl of sterile buffer (10 mM Tris, 2.5 mM $MgCl_2$, 50 mM KCl), 200 μl phenol and 10 μl 20% SDS. The phases were separated using centrifugation, and the DNA was precipitated using ethanol and resuspended in 20 μl TE (10 mM Tris [pH 8.0], 1 mM EDTA).

PCR (Polymerase Chain Reaction) was performed using the *GeneAmp*® Kit (Perkin Elmer Cetus, Norwalk, Connecticut) with 25-μl reactions: 1 μl DNA template ($\approx$ 100 ng), 2.5 μl PCR buffer, 0.5 μl each dNTP, 2 μl (50 nM) each respective forward and reverse primer, 0.125 μl *Taq* DNA polymerase and 15.25 μl water. The PCR cycling program was: 30 sec at 95°C, followed by 39 cycles of 1 min at 95°C, 2 min at 50°C and 4 min at 74°C, with 7 min at 74°C after the last cycle.

Because the 18S rDNA used was difficult to PCR amplify as a single unit, it was treated as two separate units ("front" and "back"). The front 18S rDNA portion used (a) forward primer: 5'-CTG GTT GAT CCT GCC AGT AGT-3'; and (b) reverse primer: 5'-GGT TAG AAC TAG GGC GGT ATC-3'. The back 18S rDNA portion used (c) forward primer: 5'-GAT ACC GCC CTA GTT CTA ACC-3'; and (d) reverse primer: 5'-TCC TTC CGC AGG TTC ACC-3'. These primers, a–d respectively, correspond to the base positions (a) 4–24, (b) 1385–1404, (c) 1385–1404, and (d) 2446–2463, of 18S rDNA for *Acyrthosiphon pisum* (Harris), as determined by Kwon et al. (1991).

All PCR products were cloned to contend with potentially contaminating DNA (from associated fungi, parasitic arthropods, etc.) that might be present in the hemipteran ("template") preparations. Cloning used the plasmid and competent cells supplied in the *TA Cloning*® *System* (Invitrogen, LaJolla, California), and cloning procedures followed the protocols in the instruction manual. Plasmid DNA preparations were digested with *Eco* RI and separated by electrophoresis. Candidate clones for sequencing were selected based upon appropriate size of the inserted PCR product. Confirmation of the correct 18S rDNA was determined

Table 1. Base sites used in SET 4 analysis. These most conservative informative sites were retained, as discussed in the text, after attenuation and polarization of alignment A. Sites numbers are our's for alignment A after the initial attenuation (SET 1 analysis). See text for site position and secondary structure of synonymous rRNA (sensu Kwon et al. 1991). Taxa species are given under methods, STERN represents the site expression across all treated sternorrhynchan taxa. The full sequences (>2000 sites) for all taxa are deposited in GenBank, and are available there or from us.

Taxon	53	62	66	70	79ª	152	153	159	198	241	263	454ᵇ	457	721	1025	1110	1117	1123	1251	1269
COLEO	T	A	G	T	G	A	A	C	A	C	G	G	G	G	G	G	G	G	C	T
STERN	T	G	G	T	G	C	G	C	A	C	G	G	G	G	G	T	G	G	C	C
MEMBR	A	A	G	C	A	A	A	T	A	A	A	G	T	T	T	G	G	G	T	T
CERCO	A	A	G	T	A	A	A	T	A	A	A	G	T	T	G	G	G	G	T	T
CICAD	A	A	A	T	A	A	A	T	G	A	G	G	T	T	G	G	G	A	T	T
DELPH	A	A	G	C	A	A	A	T	A	C	G	A	T	G	T	G	A	A	C	T
MIRID	A	A	A	T	A	A	A	T	G	A	A	A	G	A	T	G	A	G	C	T

ª Site 79 is homoplasious, as A, in the dipterans, *Aedes* and *Drosophila* (see Carmean et al. 1992).
ᵇ Site 454 is homoplasious within several heteropteren lineages in Wheeler et al's. (1993) data sequences.

by restriction endonuclease analysis and nucleotide sequencing. Stock cultures of clones used here are available from BCC and JDS-C at USDA, Albany, California.

Both top and bottom strands of double-stranded DNA were completely sequenced using the materials and protocols supplied with the *Sequenase*® (version 2.0) *Sequencing Kit* (U.S. Biochemical, Cleveland, Ohio), and [α^{35}S]dATP (Amresham, Arlington Heights, Illinois).

Exemplar Taxa Employed.—Sequences from our material are deposited with GenBank under acc. nos. U06474 to U06481, except for *Prokelisia marginata* (Van Duzee) (acc. no U09207). Identifications were made by RJG; voucher specimens of most of the taxa are maintained at CDFA, Sacramento, California. Families analyzed and their exemplars are:

ALEYRODIDAE: *Pealius kelloggii* (Bemis) [CALIFORNIA. *SACRAMENTO Co.:* Sacramento, Mar 1993, *Prunus lyoni* (Eastwood) C. S. Sargent]. APHIDIDAE: *Acyrthosiphon pisum* (Harris) [18S rDNA sequence ex Kwon et al. (1991), deposited in GenBank, acc. number X62623]. CERCOPIDAE: *Philaenus spumarius* L. [CALIFORNIA. *CONTRA COSTA Co.:* Pinole, 29 Jun 1993, geranium]. CICADIDAE: *Okanagana utahensis* Davis [CALIFORNIA. *SHASTA Co.:* Milford, Jul 1993, *Artemisia tridentata* Nuttall]. DELPHACIDAE: *Prokelisia marginata* [CALIFORNIA. *CONTRA COSTA Co.:* Richmond, 28 Sep 1993, *Spartina foliosa* Trin.]. DIASPIDIDAE: *Aonidiella aurantii* (Maskell) [CALIFORNIA. *SACRAMENTO Co.:* Sacramento, 14 Jul 1993, *Laurus nobilis* L.]. MEMBRACIDAE: *Spissistilus festinus* (Say) [CALIFORNIA. *YOLO Co.:* Davis, 20 Sep 1993, alfalfa]. MIRIDAE: *Lygus hesperus* Knight [CALIFORNIA. *YOLO Co.:* Davis, 20 Sep 1993, alfalfa]. PSYLLIDAE: *Trioza eugeniae* Froggatt [CALIFORNIA. *ALAMEDA Co.:* Albany, 7 Apr 1993, *Eugenia* sp.]. TENEBRIONIDAE: *Tenebrio molitor* L. [18S rDNA sequence ex Hendriks et al. (1988), deposited in GenBank, acc. number X07801].

Phylogenetic Analyses.—Initial alignments of nucleotide sequences were achieved using *Gene Works*® (version 2.3.1, subprogram: "DNA Alignment"; IntelliGenetics, Mountain View, California); final optimal alignments were done by hand. Because of the length of our nucleotide sequences, we only present those most conservative sites for Euhemiptera in Table 1; full sequences are deposited in GenBank and are available there, or from us, upon request. The 18S rDNA of

many of the hemipteran taxa, especially Sternorrhyncha, contained highly variable expansion regions. These regions were synonymous to helices 10, E21, 41 and 47 of the secondary structure of synonomous 18S rRNA of *A. pisum* (Kwon et al. 1991, Campbell et al. 1994), and were largely unalignable (< 70%) at the higher taxonomic levels studied here. Further, the 18S rDNA of several groups suggests they have a higher clock-speed base substitution rate, causing unacceptable DNA homoplasy between major clades. Because the effect of these swamped the more conservative 18S rDNA regions that were needed to decipher the ancient topology among major clades, we eliminated their influences through a sequential series of attenuations.

PAUP (Swofford 1993: vers. 3.1.1), in both "branch and bound" and "exhaustive" search modes, was used for phylogenetic analyses. Gaps and deletions were scored as missing (in SET 1, see below). Weighting (1:10) of transitions to transversion did not affect tree topologies in any analyses. The PAUP algorithm was employed because parsimony, as an optimality criterion, has been demonstrated to show the greatest accuracy in converging on a phylogenetic topology with equal rates of evolution, across the range of numbers of available base sites (especially the least), for Kimura model of evolution and a 10:1 transition : transversion ratio (Hillis et al. 1994); also see Steel et al. (1993) and Sidow/Stewart (1993) for further discussion of the parsimony criterion in nucleotide analyses. Although our taxa initially indicated differential rates of base pair substitutions among differing lineages (Campbell et al. 1994), the problem was dealt with by selective removal of ancillary groups during the analyses to eliminate these effects and increase resolution among retained taxa. Similar analytical procedures were functionally employed on problematic 18S and 28S rRNA data for metazoans and increased the resolution of their ancient phylogenetic topology (Christen et al. 1991, Lafay et al. 1992, Smothers et al. 1994), and also have been employed in phylogenetic reconstruction using continuous morphometric data that has been transformed using ordinations (Sorensen 1992).

Of many sets of PAUP analyses that were run, four sets are presented here to illustrate the effect of alignments, and of sequentially attenuating the homoplasy encountered in the 18S rRNA gene in order to eliminate all but its most conservative regions. This homoplasy was usually judged by relatively poor (1) consistency indexes and (2) bootstrap numbers (but see Hillis & Jull 1993, Felsenstein & Kishino 1993), and by (3) convergent site expression among only the more terminal taxa between established sister-clades Sternorrhyncha and Euhemiptera.

Initially, our 18S rDNA extraction of a thrips (*Frankliniella* sp.) was considered for tree rooting; however, it possessed an inordinate number of autapomorphic nucleotides, which rendered it unsuitable, given the level of 18S rDNA homoplasy in Hemiptera. We also considered a psocopteran for rooting, but were unable to amplify the full 18S rRNA gene. Ultimately, we chose an available coleopteran, because of the temporal (Permian) divergence involved, and because Coleoptera is a basal clade in the Endopterygota, the sister-group to the hemipteroid lineage (Hennig 1981, Kukalova-Peck 1991, Carmean et al. 1992). The beetle 18S rDNA was used in conjunction with that of a psyllid, because Campbell et al. (1994), and our initial analyses, determined that psyllids were the most basal group in clade Sternorrhyncha; thus, Psyllidae are the nearest monophyletic out-group for analyses of Euhemiptera.

In the first set of analyses (SET 1), all the 18S rDNA sites and all treated taxa were employed, and generated trees were anchored using the beetle. SET 1 was divided into two subsets (1A, 1B), allowing an estimation of the effect of two differing alignment orders (A, B) among their taxa. Each subset began with a different taxon as its initial nucleotide alignment, and aligned the sequentially varying remaining taxa to the first; this served as a check for potential homology among sites, as deletions were inferred during alignment. The order of alignment A (SET 1A) was: delphacid, mirid, cicada, cercopid, membracid, beetle, psyllid, diaspidid, aphid, aleyrodid; this yielded 2738 (alignment inferred) sites, of which 336 were informative. The order of alignment B (SET 1B) was: membracid, cercopid, cicada, mirid, delphacid, beetle, psyllid, diaspidid, aphid, aleyrodid; this yielded 2773 (alignment inferred) sites, of which 307 were informative. Differences in the number of sites between these alignments resulted from ambiguities in aligning sites within variable helices.

The second set of analyses (SET 2) were also conducted on all treated taxa using subsets with alignments A and B (SET 2A, SET 2B, respectively). The data from both these subsets were attenuated, however, so that all inferred site deletions were removed from each, along with all adjacent sites on both sides, back to agreement across all taxa. This provided an objective and significantly more conservative estimate of site homology and essentially eliminated subjectivity in the interpretation of ambiguously aligned sites. The SET 2A attenuation yielded 1513 sites, of which 110 were informative; that of SET 2B yielded 1494 sites, of which 100 were informative.

The third analysis set (SET 3) was conducted to eliminate the effect of site homoplasy induced by the presence of more derived taxa within clade Sternorrhyncha, some members of which have greatly accelerated base substitution rates for the gene (Campbell et al. 1994). In SET 3: the diaspidid, aphid and aleyrodid were eliminated; the nucleotides were realigned in their absence using the alignment A (most informative sites) taxon order; and the tree was anchored using the beetle. This yielded 1647 sites, of which 64 were informative. The total SET 3 site number increased over that of either SET 2 subset because deletions present in the omitted taxa, and their pruning effect, were eliminated. The SET 3 number of informative sites dropped from either of the SET 2 subsets, however, because synapomorphies among the omitted sternorrhynchans were also eliminated.

The final analysis set (SET 4) was conducted on the SET 3 taxa, but used the most severe estimate of conservative sites available within Euhemiptera. The SET 4 analysis was based upon alignment A (most informative sites), but used: (1) only those sites that could be individually out-group polarized in a Hennigian sense, and (2) of those, sites showing parallel homoplasy between Sternorrhyncha and Euhemiptera were excluded. Therefore, only those alignment A sites were used that were plesiomorphic in both the beetle and psyllid (the sternorrhynchan basal clade), but which were also nonhomoplasiously apomorphic within Euhemiptera, with respect to their lack of co-occurrence in Aleyrodiformes (diaspidid, aphid, aleyrodid, sensu Campbell et al. 1994). Sites synapomorphic throughout Sternorrhyncha, but plesiomorphic throughout Euhemiptera used, were also included to give a measure of the support for clade Sternorrhyncha. Thus, SET 4 employed the 20 most conservative informative sites. The SET 4 topology was manipulated using MacClade (Maddison & Maddison 1992), to explore its less optimal alternatives.

Topology Descriptors Used.—Here, brevity of text description for various tree topologies favors the use of a slightly modified "Newicks's 8:45" tree description standard, which is commonly used in phylogenetics. This format lists network terminals as relative nested subsets within parenthetical enclosures; for further definition, see Swofford (1993). We use curved brackets, { }, and italics to offset the descriptors from the text. For example, {{*A, B*},{*C,* {*D, E*}}} describes the topology: clade A+B as sister-group to clade C+D+E, and within the latter, sister-group C to clade D+E. We also may inject bootstrap support numbers (BSS) in the descriptors, as for example, {{*A, B*} *85, C*} *73,* where clade A+B bootstraps at 85% and clade A+B+C at 73%. We abbreviate the taxa, sometimes including larger recognized clade names where their internal topology are unimportant in the given frame of reference, by their capitalized first five letters (e.g., {{*MEMBR, CERCO*}, *STERN*} for {{*Membracidae, Cercopidae*}, *Sternorrhyncha*}).

Results: The 18S rDNA Trees

SET 1.—SET 1A, based on 2738 total sites [TS] and 336 informative sites [IS], yielded a minimum length tree [MLT] (not shown) with a tree length [TL] of 847 and a consistency index [CI] of 0.58. In that topology: {{*STERN*} *92,* {*EUHEM*} *60*}. Within Sternorrhyncha: {{{*APHID, DIASP*} *100, ALEYR*} *99, PSYLL*} *92*; which supports clade Aleyrodiformes (sensu Campbell et al. 1994). Within Euhemiptera: {{*AUCHE*} *53, MIRID*} *60.* Within Auchenorrhyncha: {{*CICAD, CERCO, MEMBR*} *96, DELPH*} *53*; as a trichotomy within Cicadomorpha, with sister-clade Fulgoromorpha. Thus, SET 1A supports an Auchenorrhyncha clade but only at BSS 53.

SET 1B (based on 2773 TS, 307 IS) yielded a MLT (not shown) with TL 773 with CI 0.57. The MLT topology for SET 1B is similar to that for SET 1A in that: {{*STERN*} *68,* {*EUHEM*} *75*}; showing lower bootstraps for Sternorrhyncha, but higher for Euhemiptera. Also, within Sternorrhyncha: {{{*APHID, DIASP*} *100, ALEYR*} *79, PSYLL*} *68*; showing lower bootstraps for the entire clade and clade Aleyrodiformes. However, SET 1B shows paraphyly for Auchenorrhyncha, with topology: {{*CICAD, CERCO, MEMBR, MIRID*} *54, DELPH*} *54*; where the heteropteran forms a quadrachotomy at low bootstrap with the cicadomorphans, and fulgoromorpha is sister-clade to that grouping.

SET 1 resolves Sternorrhyncha, its internal topology, and Euhemiptera, but does not resolve the origin of Heteroptera or potential monophyly for Auchenorrhyncha. The low CIs (0.58, 0.57) for SETs 1 indicate high homoplasy levels in the data.

SET 2.—The same two equally parsimonious MLT topologies, shown in Figs. 1A, 1B, were produced by both attenuated SET 2A (based on 1513 TS, 110 IS) and SET 2B (based on 1494 TS, 100 IS). For SET 2A, these MLT topologies had TL 232 with CI 0.59; for SET 2B, they had TL 208 with CI 0.58.

Both these SETs 2 MLTs show topology: {{*STERN*} *93,* {*EUHEM*} *97*}; the increased euhemipteran bootstrap indicates that the first attenuation of the data was successful in removing some homoplasy between it and Sternorrhyncha, due, most probably, to the unique expansion areas of the 18S rDNA in the latter (see Campbell et al. 1994). The internal sternorrhynchan topology is also preserved with reasonable bootstraps, as: {{{*APHID, DIASP*} *99, ALEYR*} *84, PSYLL*} *93.*

The two competing SET 2 MLTs, however, again differ in the placement of Heteroptera within Euhemiptera, but both indicate polyphyly for Auchenorrhyn-
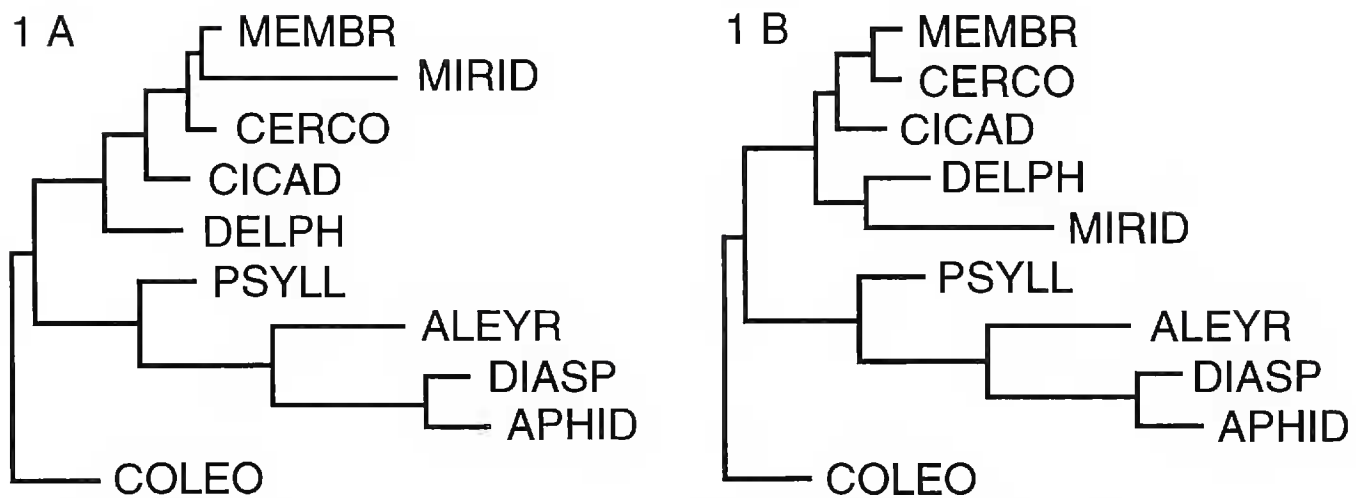
Figure 1. Two tying minimum length trees (Figures 1A, 1B) from PAUP analyses of SETs 2A and 2B. Alignments A (1513 TS, 110 IS) and B (1494 TS, 100 IS) both produced these tying MLTs. For SET 2A: TL 232, CI 0.59; for SET 2B: TL 208, CI 0.58. Branch & Bound bootstrapping for this data indicates support for clade Euhemiptera (BSS 97) and clade Sternorrhyncha (BSS 93); within Euhemiptera: quadrachotomy {MIRID, CICAD, DELPH, {MEMBR, CERCO} 52}; within Sternorrhyncha: {{{APHID, DIASP} 99, ALEYR} 84, PSYLL} 93. The Fig. 1A MLT indicates a potential origin of Heteroptera may be associated with cicadomorphans. The Fig. 1B MLT indicates clade Fulgoromorpha+Heteroptera with sister-clade Cicadomorpha. Both MLTs show internal topology for Sternorrhyncha as per Campbell et al. (1994). Topology internode lengths are proportionate to number of anagenic base substitutions present in SET 2A data set (alignment A), which is a function of the induced groups and their informative sites in the nucleotide matrix.

cha. The first topology indicates: {{{{MEMBR, MIRID}, CERCO}, CICAD}, DELPH}; with Heteroptera originating from the more terminal end of an otherwise paraphyletic Auchenorrhyncha and Cicadomorpha. The second indicates: {{{MEMBR, CERCO}, CICAD}, {DELPH, MIRID}}; with monophyly for Cicadomorpha, polyphyly for Auchenorrhyncha, and clade Fulgoromorpha+Heteroptera as sister-group to Cicadomorpha. SET 2 bootstraps for Euhemiptera show the quadrachotomy: {{MEMBR, CERCO} 52, CICAD, DELPH, MIRID} 97.

SET 2 confirms the topology of Sternorrhyncha. Within Euhemiptera, it does not resolve the origin of Heteroptera or monophyly of Cicadomorpha, Although it indicates polyphyly for Auchenorrhyncha. The low SETs 2 CIs (0.58, 0.59) continue to indicate the presence of high homoplasy levels.

SET 3.—SET 3 (based on 1647 TS, 64 IS), which eliminated all Sternorrhycha except Psyllidae, produced 945 possible trees; its MLT, with TL 117, and the next five shortest trees, with TLs 118–120, are shown in Figs. 2A–F. The SET 3 MLT topology (TL 117) for Euhemiptera shows: {{{CERCO, CICAD}, MEMBR}, {DELPH, MIRID}}; indicating monophyly for Cicadomorpha with clade Fulgoromorpha+Heteroptera as its sister-group, and polyphyly for Auchenorrhyncha. The second and third shortest SET 3 topologies confirm this, and differ only in their internal topology within Cicadomorpha, as: {{MEMBR, CICAD}, CERCO} at TL 118, and {{MEMBR, CERCO}, CICAD} at TL 119. The three topologies tying for fourth most parsimonious place, at TL 120, all place Heteroptera at various origin points within (extant) Cicadomorpha (Figs. 2D–F). Thus, the several most parsimonious SET 3 trees indicate polyphyly for Auchenorrhyncha.

SET 4.—The out-group polarized data of SET 4 (20 IS only), yielded the MLT in Fig. 3, with TL 29 with CI 0.72. In this analysis, only the most conservative informative sites available for inference of euhemipteran topology were used (see
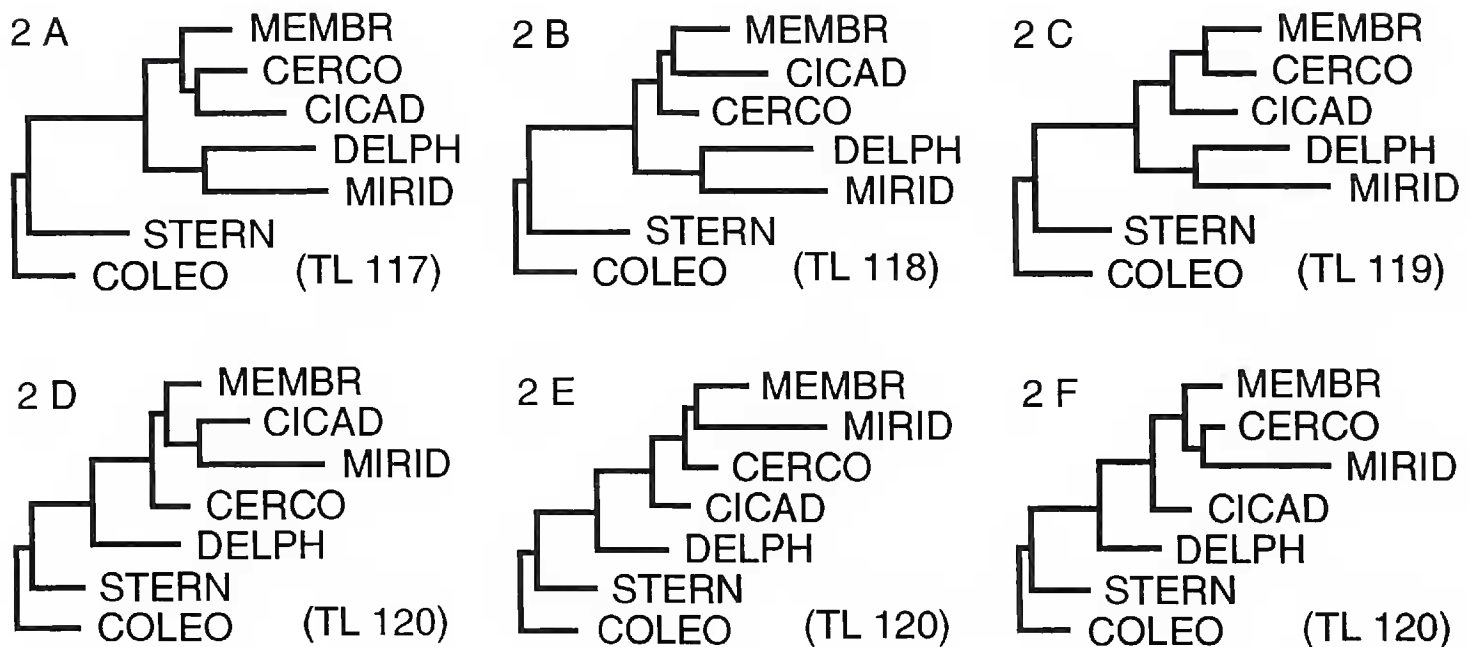
Figure 2. MLT (Figure 2A) from SET 3 PAUP analysis, based on 647 TS and 64 IS, yielding TL 117. Figures 2B–F show topologies for second (Figure 2B: TL 118), third (Figure 2C: TL 119) and fourth (Figures 2D–F: TLs 120) best levels of parsimony. The MLT plus the second and third most parsimonious topologies indicate clade Fulgoromorpha + Heteroptera with sister-clade Cicadomorpha; a heteropteran association with Cicadomorpha does not occur until the fourth best parsimony level.

methods discussion for SET 4). The MLT topology for Euhemiptera was {{{*MEMBR, CERCO*}, *CICAD*}, {*DELPH, MIRID*}}; again this indicates monophyly for Cicadomorpha, with sister-group clade Fulgoromorpha + Heteroptera, and polyphyly for Auchenorrhyncha.

Support for Non-monophyly of Auchenorrhyncha. —Given a parsimony criterion, none of our 18S rDNA analyses indicate monophyly for Auchenorrhyncha. Instead, Auchenorrhyncha was always indicated to be para- or polyphyletic because usually either Heteroptera arises: (1) as a sister-group to Fulgoromorpha, the two forming a clade that itself assumes a sister relationship to clade Cicadomorpha; or (2) from within the (then nonmonophyletic) Cicadomorpha. In fact, clade Cicadomorpha with sister-group Heteroptera is more parsimonious than clade Auchenorrhyncha.

In our most conservative and preferred analysis, SET 4, the clades in the MLT are supported by the following numbers of synapomorphies (our alignment A numbers for SET 2 sequences, first attenuation), with transitions indicated by * and transversions by ** (Table 1). Sternorrhyncha: 5 nonhomoplasious unambiguous synapomorphies (sites: 62 [A → G*], 152 [A → C**], 153 [A → G*], 1110 [G → T**], 1269 [T → C*]). Euhemiptera: 2 nonhomoplasious unambiguous synapomorphies (sites: 53 [T → A**], 159 [C → T*]), plus potentially 2 homoplasious ambiguous synapomorphies (sites: 241 [C → A**] with reversal in Delphacidae, 457 [G → T**] with reversal in Miridae); the latter two ambiguities are equivocal in support of either Euhemiptera or Cicadomorpha, however; in addition, site 79 [G → A*] is apomorphic for the Euhemiptera, but is homoplasious with some Diptera (see Table 1, also see Carmean et al. 1992). Cicadomorpha: 2 nonhomoplasious unambiguous synapomorphies (sites: 721 [G → T**] with independent mutation in Miridae [G → A*], 1251 [C → T*]); also potentially plus the two ambiguous sites stated to be equivocal for Euhemiptera. Clade Cercopidae + Membracidae: 1 homoplasious unambiguous synapomorphy (site: 263 [G
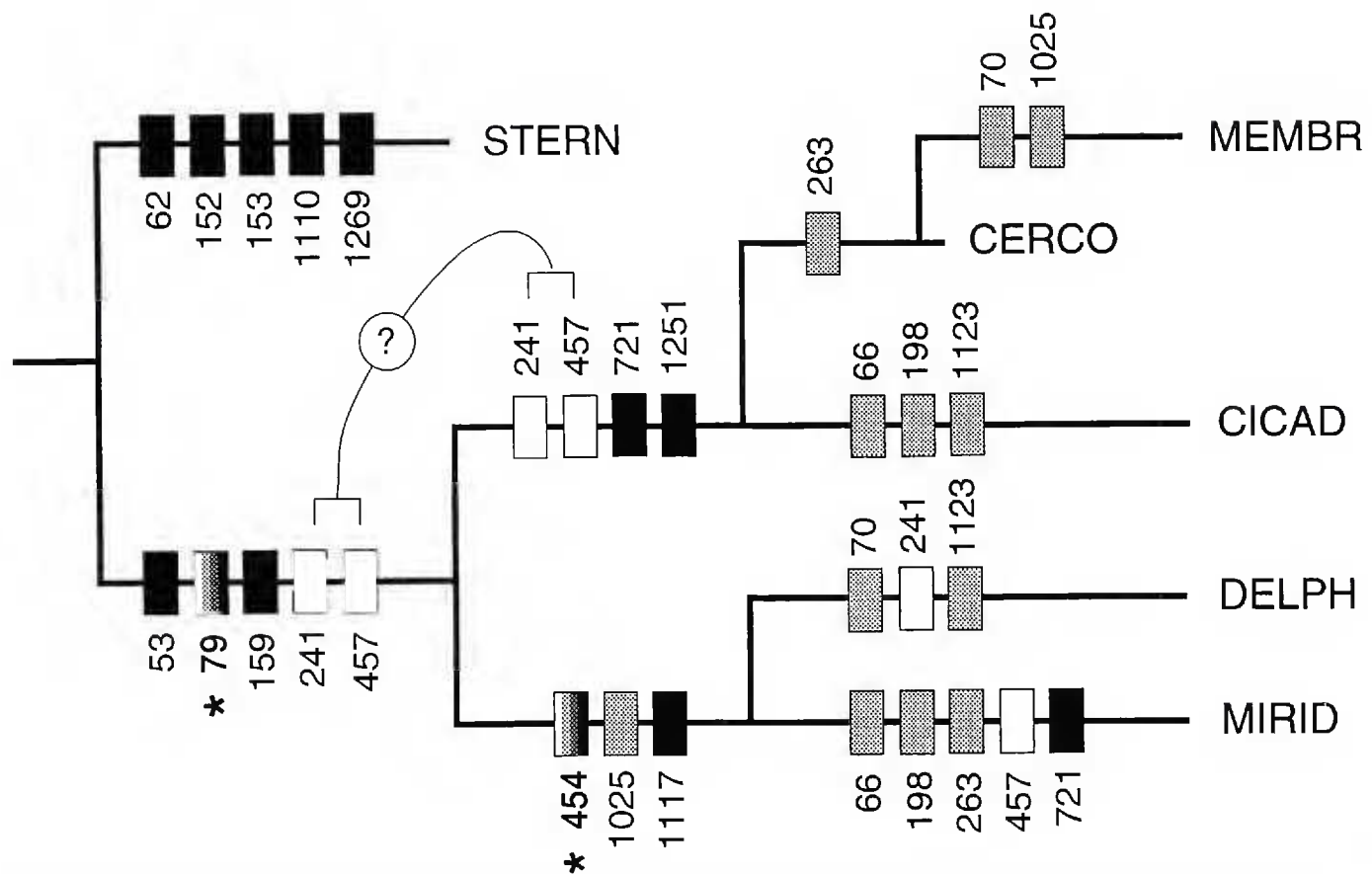
Figure 3. MLT produced from the SET 4 data set (20 IS only), where sternorrhynchan homoplasy was excluded using out-group polarization. Bars on internodes represent synapomorphies labelled with their site numbers (Table 1); black = nonhomoplasious and unambiguous site change; gray = homoplasious (within Euhemiptera) but unambiguous site change; white = homoplasious (within Euhemiptera) and ambiguous site change. Sites 79 and 454 (white to black gradients with asterisk) are homoplasious outside this analysis; 79 is homoplasious in dipterans and 454 in some heteropteran lineages (see Table 1). Sites 241 and 457 are ambiguous site changes, marked by ?, that may occur either along the euhemipteran ancestral internode, or alternatively along the cicadomorphan ancestral internode. Site 721 is an independent transformation on the cicadomorphan and heteropteran ancestral internodes. The MLT supports clade Fulgoromorpha+Heteroptera.

→ A*] parallelism in Miridae). Clade Fulgoromorpha+Heteroptera: 1 nonhomoplasious unambiguous synapomorphy (site: 1117 [G → A*]) and 2 homoplasious unambiguous synapomorphies (sites: 454 [G → A*], homoplasious within heteropterans in Wheeler et al's. (1993) sequences, and 1025 [G → T**], a parallelism in Membracidae). Although the single representatives for Fulgoromorpha and Heteroptera used were thought to preclude informative sites as synapomorphies for them, Heteroptera showed the mentioned independent mutation of site 721 [G → A*]. (Synapomorphies for each of Fulgoromorpha and Heteroptera are available in our subsequent analyses, see footnote 7).

In the SET 4 MLT, clade Fulgoromorpha+Heteroptera precludes Auchenorrhyncha monophyly, yet it is based on 1 *nonhomoplasious transition* synapomorphy (site 1117) and (in "opposition") 2 *homoplasious* synapomorphies, a *transition* (site 454) showing homoplasy in some heteropteran lineages (Wheeler et al. 1993), and a *transversion* (site 1025). Some authors suggest transversion/ transition mutation biases are present in some nucleotide data (e.g., primate mtDNA), and that a 10:1 weight should be imposed in favor of transversions for phylogenetic inference (Mishler et al. 1988, Patterson 1989, Michevich & Weller 1990). If so, such weighting could affect MLT generation towards a topology optimizing transversions over transitions. In fact, even a philosophical preference towards a transversion bias should tend to negatively affect the relative acceptance

of a topology where transitions appear to dominate over tranversions on given cladogram internodes (e.g., clade Fulgoromorpha+Heteroptera on the SET 4 MLT).

However, 18S rDNA does not appear to show such bias for those secondary structural portions of the molecule termed "bulges" or "loops" (Vawter & Brown 1993). The transition synapomorphy of clade Fulgoromorpha+Heteroptera occurs on such a secondary substructure. Our site 1117 (= site 1715 of Kwon et al. 1991) occurs on a "bulge" (Kwon et al. 1991: fig. 3, bulge position of helix 40), where a transversion bias was not present for 18S rDNA (Vawter & Brown 1993). Thus, for our 18S rDNA sequences, equal weights for transitions and transversions are appropriate, so that a prejudice against the SET 4 MLT is unreasonable.[7]

Nevertheless, as an alternative to the SET 4 MLT, we explored other, less parsimonious SET 4 topologies that would permit monophyly for Auchenorrhyncha. Using PAUP and the SET 4 data, we tabulated the probability of monophyly for Auchenorrhyncha and other groups sequentially across all possible TLs (29–42), as decreasing levels of parsimony (Table 2). For each rising TL level, we noted the accumulative numbers of trees containing each of 5 possible clades: (a) Euhemiptera, (b) Cicadomorpha, (c) Cicadomorpha+Heteroptera, (d) Fulgoromorpha+Heteroptera, and (e) Auchenorrhyncha; any internal topology was permitted for the member taxa of each "clade." These accumulations were transformed to probabilities (of existence) for the clades, as their frequency of occurrence (i.e., the accumulated total number of trees containing a clade at each TL, divided into the number of trees possible at that TL). The probabilities of clades Cicadomorpha+Heteroptera and Fulgoromorpha+Heteroptera, and their total, can also be taken as a function of probability for non-monophyly for Auchenorrhyncha, because of conflicting relative association of Heteroptera. In Table 2, clade Auchenorrhyncha does not exist until the third best parsimony level (TL 31), where it occurs on only 2 of 23 possible trees (0.09), and that by that level, competing clades Fulgoromorpha+Heteroptera (0.52) and Cicadomorpha+Heteroptera (0.39) both occur at greater frequencies (Σ 0.91). Auchenorrhyncha rises to its greatest frequency (0.18) at TL 32, where it remains the least probable clade; it rises to its greatest occurrence (30 trees of 822 retained and 945 possible) at TL 38, where it ties with competing clade Cicadomorpha+Heteroptera

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[7] This synapomorphy is supported in additional analyses involving a more extensive sampling of taxa (Campbell et al., unpublished data), to be published elsewhere: [GenBank accession numbers in parentheses] Cercopidae-Tomaspinae (U16264), Cicadellidae-Cicadellinae (U15213), Cicadellidae-Deltocephalinae (U15148), Cixidae (U15215), Dictyopharidae (U15216), Flatidae (U06476), Gerridae (U15691), Issidae (U15214), Lygaeidae (U15188). Given the fact, in matrix generation of MLTs, that holding character number constant, and either decreasing average state number or increasing terminal taxa number, effectively increases the probability of homoplasy, we chose here to increase the total number of 18S rDNA base pairs analyzed to maximize the discovered synapomorphies. Based on the distribution of synapomorphies throughout differing regions of the 18S rDNA gene, it may not be possible to infer accurate phylogenetic conclusions using short segments (i.e., 6-700 base pairs) of the gene. We have compared our sequences with those of Wheeler at al. (1993) and Carmean et al. (1992) for site homoplasy. Functionally, "throwing more taxa" at this problem will merely (a) validate, or negate, the existing synapomorphies among the presented basal topology, (b) supply synapomorphies for morphologically obvious clades (e.g., Fulgoromorpha), or (c) permit insertion of excluded taxa (e.g. Coleorhyncha). The Campbell et al. (to be published) analyses, which increase taxa, will verify non-monophylly for Auchenorrhyncha and discuss mutation rate differences for regions of the 18S rDNA gene. *See note added at end of Literature Cited.*

Table 2. Accumulative frequency of selected "clades" across all tree lengths for 945 possible trees from SET 4 data.

	Tree length													
	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Trees generated[a]	1	9	23	51	74	109	127	169	244	383	582	700	791	822
Euhemiptera	1	9	23	50	72	99	103	105	105	105	105	105	105	105
	(1.00)	(1.00)	(1.00)	(0.98)	(0.97)	(0.91)	(0.81)	(0.62)	(0.43)	(0.27)	(0.18)	(0.15)	(0.13)	(0.13)
Cicadomorpha	1	4	8	10	11	15	23	35	35	35	35	35	35	35
	(1.00)	(0.44)	(0.35)	(0.20)	(0.15)	(0.14)	(0.18)	(0.21)	(0.14)	(0.09)	(0.06)	(0.05)	(0.04)	(0.04)
Cicadomorpha+	0	5	12	15	15	22	26	30	30	30	30	30	30	30
Heteroptera[b]	(0)	(0.56)	(0.52)	(0.29)	(0.20)	(0.20)	(0.20)	(0.18)	(0.12)	(0.08)	(0.05)	(0.04)	(0.04)	(0.04)
Fulgoromorpha+	1	4	9	16	17	17	17	23	46	54	78	78	78	78
Heteroptera	(1.00)	(0.44)	(0.39)	(0.31)	(0.23)	(0.16)	(0.13)	(0.14)	(0.19)	(0.14)	(0.13)	(0.11)	(0.10)	(0.09)
Auchenorrhyncha	0	0	2	9	11	16	18	22	25	30	30	30	30	30
	(0)	(0)	(0.09)	(0.18)	(0.15)	(0.15)	(0.14)	(0.13)	(0.10)	(0.08)	(0.05)	(0.04)	(0.04)	(0.04)

[a] Retained.

[b] Any internal topology allowed among member taxa.

for fewest tree numbers. Thus, given the conservative data of SET 4, which was designed to optimally eliminate the more recently derived homoplasious sites that obfuscate evolutionary topological relationships among the older clades, we find scant evidence for the possibility of monophyly for Auchenorrhyncha.

CLADISTIC IMPLICATIONS

Until now, Auchenorrhyncha was generally considered to be monophyletic on the basis of either molecular data from insufficient subgroups (Wheeler et al. 1993), or morphological traits previously considered to be valid synapomorphies (but see Hamilton 1981). A recent example of the latter is Carver et al.'s (1991: 464) statement that "The monophyly of the Auchenorrhyncha . . . is firmly established by the complex tymbal acoustic system and the aristoid antennal flagellum characteristic of the group." Other traits across Auchenorrhyncha have been considered symplesiomorphies, with the exception of a fused ScP+R vein apomorphy (Kukalova-Peck 1991: 170).

However, phylogenetic reconstruction using nucleotide sequencing is thought to be superior to, and definitely more objective than, that based upon morphology (Felsenstein 1982, 1983, 1988; Crespi 1992; Sorensen 1992). This is because, in general, nucleotide substitutions are random, non-selective events, as opposed to trying to determine how to code and weight morphological characters, which are defacto a result of selection. Morphologically-based phylogenetics is conceptually plagued by the inherent effects of selection and character correlation; although these are easily recognizable, they are nearly impossible to handle (see Sorensen 1990, 1992). Use of nucleotides not only renders a portrait that is essentially free of these problems (Lewontin 1989), but permits character transformation overlays that allow recognition of morphological homoplasy. If the 18S rDNA phylogeny derived here is correct, it is evident that the morphological synapomorphies for Auchenorrhyncha must be convergences that are most probably selection-induced.

Tymbal Systems as Homoplasy. —Although the development of a complex tymbal system for sound production may seem like a strong synapomorphy for Auchenorrhyncha, this mechanism is homoplasious in Hemiptera and clearly is under strong sexual selection. Tymbal systems not only exist in Cicadomorpha and Fulgoromorpha, but they also occur in Pentatomomorpha (e.g., Pentatomidae: *Carpocoris*; Chapman 1971), a highly derived and phylogenetically distant clade (Wheeler et al. 1993), where their position and function appears to be similar to that within most Auchenorrhyncha. Furthermore, despite many investigations into tymbal sound production in various Auchenorrhyncha (Ossiannilsson 1949, Smith & Georghiou 1972, Shaw & Carlson 1979, Mitomi & Okamoto 1984, Zhang & Chen 1987, Zhang et al. 1988), except for Cicadidae (Pringle 1954, 1957), precise and convincing physiological mechanisms of their function in leafhoppers or planthoppers have not yet been published (Claridge 1985, Claridge & de Vrijer 1994) and remain, at best, controversial.

In Ossiannilsson's (1949: 103–106) discussion of morphology, there are many significant differences between the fulgoromorphans (Delphacidae [as "Areopidae"], Cixidae, Issidae) and cicadomorphans (Cercopidae, Cicadellidae, Membracidae) that he examined. Examples of these differences include Fulgoromorpha's lack of (a) a "striated tymbal" (shared with some cicadellids) and (b) a "pilose surface"; their (c) "enlarged metapostnotum," (d) "less developed meta-

postphragma," (e) "well developed lateral dorsal longitudinal muscles" (except in brachypterous forms); their (f) "second abdominal tergum" being "devoid of phragmata in spite of the dorsal longitudinal muscles of the first abdominal segment being strongly developed"; and their (g) "second tergum being strongly vaulted into a convex, shield-like surface with inner strengthening lists," which serve as the posterior attachment of the longitudinal muscles from the metapostnotum.

Perhaps the best reference to Fulgoromorpha's tymbal variance is summarized by Ossiannilsson's (1949: 104) statement that homology across the Auchenorrhyncha for muscle $I\ a\ dvm_1$ ". . . might be uncertain for only the Fulgoromorpha, as the conditions of this group are so deviating . . . ." It should be evident that this uncertain homology between fulgoromorphan and cicadomorphan tymbal systems does not seem adequate to be regarded as a convincing synapomorphy for these groups, especially in light of the occurrence of an (at least superficially) similar tymbal mechanism in the Pentatomomorpha. Clearly more detailed tymbal comparisons are needed.

Aristoid Antennae as Homoplasy.—It is easier to accept the reduction to an aristoid antennae among the auchenorrhynchan groups as homoplasy if one remembers that all Pterygota and Thysanura have *annulated* (or *flagellar*) antennae (sensu Schneider 1964: type B; Chapman 1971: type A), as opposed to true *segmented* antennae (sensu Schneider 1964: type A; Chapman 1971: type B), which occur in the apterogote subclasses Collembola and Diplura. In segmented antennae, each true segment, including the scape, pedicel and each flagellar segment has up to five intrinsic muscles connecting its base to the base of the next distal segment, and these permit intersegmental movement. In annulated antennae, however, only the scape has such segmental musculature, whereas each flagellar "segment," all of which are actually mere annulations, is connected to the next by membrane only; annulated antennae are moved only by levator/depressor muscles connecting the anterior tentorial arms to the scape, and flexor/extensor muscles connecting the scape to the pedicel (Imms 1940). Thus the flagellum of the Pterogota is a single, functional unit that has already undergone reduction from true segmentation to mere annulation, and it has undergone many homoplasious further reductions across diverse taxa (i.e., larval Holometabola, adult Mallophaga/Anoplura, adult Brachycera/Cyclorrhapha Diptera, etc.).

Among hemipterans, only those that jump have evolved aristoid flagella. However, differing forms of flagellar reduction occur independently at least twice in Hemiptera (i.e., Peloridiidae and Nepomorpha) besides that noted in Auchenorrhyncha. Cicadomorphan and fulgoromorphan convergence towards an aristoid antenna results, we believe, from selection to: (a) minimize injury; (b) enhance aerodynamic streamlining; and/or (c) allow acoustic receptions via Johnston's organ. Because of its sensory function, selection to avoid or minimize antennal damage should be an extremely strong force. Antennal injury should be lessened during the less controlled, head-first landings encountered in jumping. Further, jumping with large antennae would enhance aerodynamic instability in small, bullet-like auchenorrhynchans that leap with almost explosive force (K. G. A. Hamilton, personal communication). In contrast, the more massive bodies of larger jumpers with long antennae (e.g., orthopteroids) probably minimize antennal contributions toward instability.

Aristoid flagella on hemipterans occur only in the presence of tymbal transmissions systems, but not the reverse (e.g., Pentatomomorpha). Thus, aristoid antennae may also serve as an acoustic reception device, picking up air-transmitted vibrations and transferring them to Johnston's organ, a chordotonal organ in the antennal pedicel. Although many Auchenorrhyncha apparently transmit sound through the substrate, the acoustic receptors remain largely unknown (Claridge 1985), but Johnston's organ has been suggested as such a receptor (Howse & Claridge 1970), and clearly serves such a function in other insects (Chapman 1971).

If the development of the scape+pedicel versus the flagellum are considered, the antennal systems of cicadomorphans and fulgoromorphans appear only superficially similar in their respective ultimate development. The fulgoromorphan pedicel is exceptionally developed (e.g., Hamilton 1981: figs. 18, 19), with numerous autapomorphic plaque sensilla (e.g., Baker & Chandrapatya 1993: figs. 1, 2) that vary across the group (Marshall & Lewis 1971). Fulgoromorphan flagellar annulation is generally extreme, appearing as mere thin rings, except for a relatively enlarged, bulbous flagellomere 1 (= antennal 3) (e.g., Baker & Chandrapatya 1993: fig. 6), which has an autapomorphic sensory organ (Bourgoin 1985: fig. 2, "OSBF") throughout the group.

Supportive evidence for the homoplasious evolution of an aristoid antenna in fulgoromorphans is provided inadvertently by *Megaleurodes megocellata* Hamilton (1990: fig. 34), a fossil from Brazilian Lower Cretaceous deposits (AMNH type 43608). Hamilton (1990: 96) thought it was a primitive whitefly with fulgoromorphan traits, and assigned it to "Aleyrodoidea: Boreoscytidae?". However, the traits with which *M. megocellata* was assigned to Aleyrodidae are either quite homoplasious in Hemiptera (e.g., divided eye, ocellar position) or symplesiomorphies (K. G. A. Hamilton, personal communication). Because of its facial carinae, tegulae and three-segmented tarsi (the latter two symplesiomorphies) we believe it is a primitive fulgoromorphan that shows non-aristoid antennae that arise fairly high on the face. Therefore, we tentatively reassign *Megaleurodes megocellata* to the fossil superfamily Fulgoridioidea, but with an uncertain family assignment. It is similar to the Jurassic Fulgoridiidae (sensu Bode 1953) in that its antennae are multiarticulate (non-aristoid), a diagnostic plesiomorphy for that (gradistic ?) family (Bode 1953, Hamilton 1990); but the head of *Megaleurodes* differs from that of *Fulgoridium* (Bode 1953: fig. 143) with its ocelli below the eyes (K. G. A. Hamilton, personal communication). We consider the fossil Fulgoridioidea to be an extinct grade to the modern Fulgoroidea, within Fulgoromorpha, and to demonstrate the lineage initially had non-aristoid antennae.

In contrast, in many cicadomorphans, the antenna generally has a less developed scape and pedicel and a less reduced flagellum, where flagellar annulation ("segmentation") is still usually quite evident (e.g., Cwikla & Freytag 1983: fig. 4). In some cicadas, the flagellum is still reasonably developed (e.g, Hamilton 1981: fig. 14), especially in nymphs (e.g., Hamilton 1981: fig. 2), which retain a developed, definitely "segmented," but short flagellum. Interestingly, Cicadas do not jump, and their tympana also serve as acoustic receptors. Nevertheless, some cercopids have an aristoid antennal flagellum that appears to approach that of Fulgoromorpha. These have flagellomeres 2-*n* quite annulated and an enlarged flagellomere 1, possibly with a sensory organ that externally appears somewhat similar

to that of fulgoromorphans. Shcherbakov (1988), however, states that fossil Pro-cercopidae and Karajassidae, the initial cercopoids and cicadelloids, respectively, retained a "segmented" antennal flagellum. This would necessarily indicate a more recent, independent derivation of the cicadomorphan arista than would have to occur if it was synapomorphic on a postulated monophyletic auchenorrhynchan ancestral stem.

If our 18S rDNA inferred relationships between Fulgoromorpha and Cicado-morpha are correct, homoplasy for aristoid flagellar development is required. The fulgoromorphan-like antennae of cercopids appears necessarily unparsimonious on any cladogram containing extant taxa, with sister-group Fulgoromorpha and any internal topology for Cicadomorpha (unpublished data); the early fulgoro-morphans present a similar problem. If aristoid antennae were derived only once, on the euhemipteran ancestral phylogenetic internode, the character requires at least two-steps on the 18S rDNA-based topology, with a reversal on the heter-opterodean ancestral internode; independent derivation on each of the ancestral internodes for cicadomorphans and fulgoromorphans is equally parsimonious.

Fused ScP+R Vein. —Kukalova-Peck, following her own venation terminology (Kukalova-Peck 1983), which is also used here, states that for Auchenorrhyncha, ScP- supports R, as a fusion apomorphy (Kukalova-Peck 1991: 170). She notes that in Heteropterodea, however, ScP- is independent of R, as a symplesiomorphy; yet she also shows an apomorphic ScP+R fusion in the Coleoptera (Kukalova-Peck 1991: fig. 6.28E) in the hindwing (the beetle flight wing). Dworakowska (1988) reviews the venation of Auchenorrhyncha, following Kukalova-Peck's ter-minology, and details many auchenorrhynchan wings, but her excellent study shows the limitations of homological interpretation of venation. Also see Wootton (1979) for discussion of problems in determining vein homologies.

Although the auchenorrhynchan fusion of ScP+R seems reasonable as a syn-apomorphy, we believe that it is a homoplasy. Convergence in venation occurs commonly in hemipterans (Wootton & Betts 1986), particularly among their early fossils (Wootton 1981), and is probably related to selection for various flight dynamics parameters (Betts 1986a, b, c). The auchenorrhynchan ScP+R fusion probably results from selection for rigidity in the basal region of the wing, coupled with the developing need for a point or area of flexion, just beyond, near midpoint of the forewing margin. These modifications of the primary flight wing are required for camber control during flight in heteropterans (Wootton & Betts 1986; Betts 1986a, b, c). Function-based similarities in wing geometries also appear to have been derived in more phylogenetically advanced orders, for example Hymenoptera (see Whitfield & Mason 1994: figs. 3–8). Another function-based homoplasy is the development of an expansion of the wing's precostal strip, to form an epi-pleuron in Auchenorrhyncha and Coleoptera (Kukalova-Peck 1991: 167).

To promote greater flight efficiency, we believe differing wing geometries were evolved and tested among early hemipterans. This resulted in structural conver-gence in response to the selective constraints imposed by physical factors. We feel such homoplasy can often be recognized by subtle differences among clades, however. For example, where ScP eventually reaches the forewing margin in Cicadomorpha, a venation break occurs where component C should merge smoothly with liberated component ScP, as occurs in Fulgoromorpha. To illustrate this point, consider the modifications of the three veins of the costal (pronating)

complex, while bearing in mind the auchenorrhynchan ScP+R fusion. As Pc, CA (= C+) and CP (= C−), these veins usually form a relatively tight beam-like triad along the leading edge of the fulgoromorphan forewing (Dworakowska 1988: figs. 3–5 cross-sections). This wing-leading "beam" is undoubtedly for structural reinforcement.

In some groups (e.g., Eurybrachyidae, Flatidae, Lophopidae, Nogodinidae, Ricaniidae, Tropiduchidae, some Fulgoridae; Dworakowska 1988), Pc rolls ventrally to more closely associate with CP (as fused Pc+CP), which leaves CA alone to form the forewing's functional anterior margin. However, CP never exists separately at the wing base. In Fulgoromorpha, when CP posteriorly separates from CA more distally, CP gives rise to several serial branches along the wing's anterior margin. This is what Kukalova-Peck (1991: 170) refers to as a false 'subcosta'. In such instances among fulgoromorphans, where this posteriorly moved and serially branched CP occurs, ScP+R splits distally, and shortly thereafter the liberated ScP curves to the forewing's anterior margin to fuse with CP, as ScP+CP (Dworakowska 1988: figs. 29, 37c, 41, 67); meanwhile, the abandoned R component continues distally to the wing margin, also to split as RA and RP (and usually each again). In contrast, in Cicadomorpha, where CP remains nearer the anterior margin of the forewing throughout its course, this C/ScP abutment occurs as an unfused association (Dworakowska 1988: figs. 94, 97).

Clearly structural selection is involved in this difference because the cicadomorphan situation promotes flexibility at that point along the wing margin. The homoplasious coleopteran ScP+R fusion allows hind(flight)wing folding under their elytra, with the appropriate articulation. It may also be possible that the auchenorrhynchan ScP+R fusion merely reflects a strengthening of the front-basal or proximal area of the wing, enabling CP to travel distally to its ultimate fusion/abutment with the ultimately liberated ScP, allowing the nodal flexion point. If so, it should not be surprising that in some auchenorrhynchans, proximal fusions of ScP and R with M also occur, permitting even greater stiffening, as either ScP+R+MA (Dworakowska 1988: fig. 42), or, particularly among fossils, ScP+R+M (?) (Hamilton 1990: figs. 6, 41, 42, 58, also apparently 31, 33, 65, 69, 74, 75).

In some Fulgoromorpha, the ScP+C fusion point marks the distad border of tegminization (e.g., Hamilton 1990: fig. 52), or an apparent "pterostigma" in some fossils (e.g., Hamilton 1990: figs. 46A, 55, 56, 58, 75, 80). In Cicadomorpha, the C/ScP abutment break marks a quite primitive line of flexion (Hamilton 1990: fig. 31, "Cicadoprosbolidae"; Dworakowska 1988: figs. 92, 93, 95). It is the anterior of the flexion line that permits camber change during the wing beat (Wootton & Betts 1986), and as such is under strong selection pressures.

Within clades Fulgoromorpha and Cicadomorpha, many other venation associations or fusions change, at least in part, sometimes quite notably. For instance, the free base of Sc in Cercopoidea and Cicadoidea (Shcherbakov 1981: 66), or Pc+C+Sc+R amalgamation in some cicadas (Carver et al. 1991: fig. 30.4f). We believe that these differences between cicadomorphans and fulgoromorphans serve to: (a) cloud the potential questions of homology; (b) demonstrate the "dancing," but functionally related, fusion of the axial unit-radial complex veins (sensu Dworakowska 1988) among auchenorrhynchans; and (c) illustrate the apparent need of fusion in that region of the membranous wing of these highly

active insects, to achieve rigidity among the more basal components of these veins.

In the other hemipteran clades, selection for a convergent ScP+R fusion may have been alleviated by non-active habits or differential wing evolution. Sternorrhynchans are smaller, often with "passive" flight. Coleorhynchan forewing venation is often quite thickened and pronounced (Kukalova-Peck 1991: fig. 6.25J; Popov & Shcherbakov 1991: figs. 9, 10, 12, 22, 23, 35). Among the more derived Heteroptera, the wing may be quite sclerotized proximally, with a developed cuneus and costal fracture, while among the basal heteropteran Enicocephalomorpha, which have relatively membranous wings, it is the forewing venation that is thickened.

Morphological Synapomorphies Supporting the 18S rDNA Tree.—The understanding of "homopteran" phylogenetic topology has always been plagued by an abundance of character homoplasy within and among groups, and the dearth of convincing morphological synapomorphies indicating the relationships among the major clades; the latter appears to be an artifact of limited local perspective (sensu Sorensen 1992). The 18S rDNA topology here cannot "correct" these problems; it can merely illustrate those few nonhomoplasious synapomorphies that appropriately structure the topology of the corresponding *morphological* tree. We disagree with methods employed elsewhere (e.g., Wheeler et al. 1993), wherein combinations of molecular and morphological traits are used in the same analyses to increase phylogenetic resolution. We find such character amalgamations to be philosophically and pragmatically untenable. We consider a combinable-component approach (i.e., Bremer 1990, Lanyon 1993) among various competing topologies that are based on differing dataset types, as appropriate to define topological reliability, if required. We have avoided a separate, comparative morphological analysis here, however, because we concur with Felsenstein (1988), at least in this case, that morphological characters for phylogenetic inference are inherently problematic. For example, we believe that a meaningful, morphologically-based phylogenetic analysis of hemipterans must, at the very least, reflect an apriori understanding of their historical homoplasies, as well as their coding/scoring consequences, and must appropriately include all fossil taxa.

The morphological synapomorphies that support the 18S rDNA-based topology follow, as developments (gains), unless otherwise noted. *Clade Sternorrhyncha*—(a) a sternorrhynchan-type filter chamber (Evans 1963: type A); see Fig. 3 and Campbell et al. (1994) for 18S rDNA synapomorphies. *Clade Euhemiptera*—(a) a vannus (Wootton & Betts 1986); (b) pronounced separation of costal and subcostal basivenale (Kukalova-Peck & Brauckmann 1992); (c) loss of ScA+ vein (Kukalova-Peck & Brauckmann 1992). *Clade Cicadomorpha*—(a) a cicadomorphan-type filter chamber (Evans 1963: type B); (b) a ledge overhanging the antennal insertion (Hamilton 1981; K. G. A. Hamilton, personal communication); (c) the lorum with a wide connection to hypopharynx and a very narrow connection to the gena (Hamilton 1981; K. G. A. Hamilton, personal communication); and (d) a spiral-fold or -lobed wing-coupling system (D'Urso & Ippolito 1994: type A), modified from the sternorrhynchan system wherein one or more spiral hooks occur instead (D'Urso & Ippolito 1994: 223). *Clade Fulgoromorpha+Heteropterodea*—(a) slight reduction of the lorum (Hamilton 1981), as intermediate step to Heteropterodea (K. G. A. Hamilton, personal communication);

(b) apical fusion of forewing veins 1A and 2A (Wootton & Betts 1986); (c) a long and longitudinally-directed forewing vein CuA (Wootton & Betts 1986); questionably (e) often strong microspines, as accessory microsculpture, on the vein opposite the fold of the wing-coupling apparatus (D'Urso & Ippolito 1994: 223); and (d), of uncertain polarity, lack of a hindwing ambient vein; also, although polarities are uncertain, we suspect that several alimentary canal modifications shared by Fulgoromorpha, Coleorhyncha and Heteroptera (Goodchild 1966) represent plesiomorphies for a gut that lacks any filter chamber type—these include a 'pylorus', a sac-like rectum, reduced rectal glands, and a midgut-hindgut junction situated posteriorly in the body cavity. *Clade Fulgoromorpha*—(a) specialized facial carina (Hamilton 1981); (b) a collar-like pronotum (Hamilton 1990); (c) placate sensilla on the pedicel (Baker & Chandrapatya 1993); (d) a specialized sensory organ on the base of flagellomere 1 (Bourgoin 1985); (e) a rolled, but never spiral, folded wing-coupling system (D'Urso & Ippolito 1994: type B), with (f) strong accessory microsculpture. *Clade Heteropterodea* (= Coleorhyncha+Heteroptera)—(a) a gula, or the beginning of its ventral fusion in Coleorhyncha (Hamilton 1981: fig. 23); (b) a distinctive triangular mandibular lever (Hamilton 1981; K. G. A. Hamilton, personal communication); (c) a non-aristoid reduction of antennae to 3 or 4 (secondarily 5) segments (Schlee 1969, Emel'yanov 1987, Wheeler et al. 1993); (d) capture of the trachea of forewing vein 1A by CuA2 and its invasion of the remigium (Wootton 1965, 1986), despite Wootton's (1979) summary of unreliability of tracheal capture for vein homology; (e) wings capable of being folded flat (overlapping) over the body (Wheeler et al. 1993); (f) ground plan for the abdominal segments (Schlee 1969); (g) structure of the anal cone (Schlee 1969); and (h) development of the sclerites at the base of the aedeagus (Schlee 1969); see Wheeler et al. (1993) for 18S rDNA synapomorphies. *Clade Coleorhyncha*—see Popov & Shcherbakov (1991: 233) for synapomorphies. *Clade Heteroptera*—see Wheeler et al. (1993) or Hennig (1981) for numerous synapomorphies.

Paleontological Evidence

Under the section on cladistic implications, we considered some fossil evidence for character homoplasy. Here, we estimate the concordance of fossil lineages with the 18S rDNA topology.

Prior to 1980, the relationships among hemipteran fossils were confused by differing philosophical camps that often made interpretations despite a lack of important character information. In a review article, Wootton (1981: 331–332) states: "Within the Permian, Hemiptera radiated spectacularly, leaving behind a bewildering array of fossils, many of them just wings. Convergence is widespread, and interpretation difficult and conflicting. . . . Auchenorrhyncha occur in profusion and confusion in the L. and U. Permian . . ."; he cites as an example: "Prosbolidae may be primitive Cicadoidea, and Scytinopteridae may be Cercopoidea, but both these families have been conflictingly defined" (e.g., Evans 1956, 1964, vs Rohdendorf et al. 1961, Bekker-Migdisova in Rohdendorf 1962). Hennig (1981: 273) aptly summarizes: "The differences of opinion do not inspire me with much confidence in the decisions of specialists who have assigned the Permian and other fossils to various subgroups of *Auchenorrhyncha." There was no apparent rigorous cladistic methodology for assignments and homology. Usually,
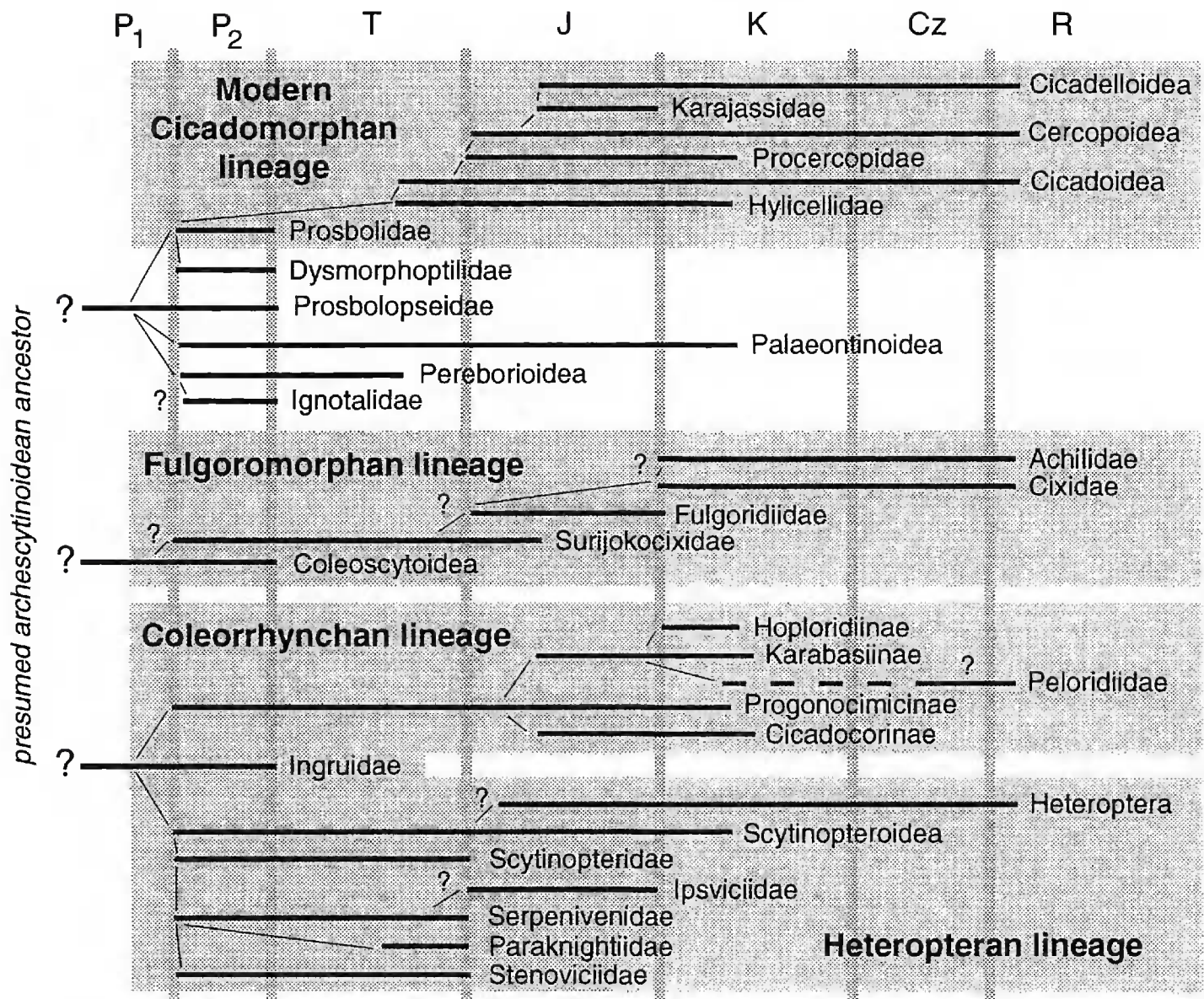
Figure 4. Paleontological synopsis of (selected) taxa from euhemipteran lineages, largely following Shcherbakov (1984, 1988) and Popov & Shcherbakov (1988, 1991) with insertion of Fulgoridiidae (Bode 1953, Hamilton 1990). Abbreviations for geological times are standard; gray boxes demarcate clade lineages; question marks (small and large) signify derivations implied as tenative in the literature. Shcherbakov (1984) places Prosbolopseidae and Ingruidae in superfamily Prosboloidea.

early hemipterans were known only from forewing tegmina; body and head impressions, sometimes distorted, usually are unknown until the Jurassic (e.g., Bode 1953, Hamilton 1990). However, despite this reliance on tegmina, only Evans (1964) attempted to define early fossil auchenorrhynchan superfamilies by wing venation.

More recently, Shcherbakov (1981, 1982), following Emel'yanov (1977), and Dworakowska (1988), following Kukalova-Peck (1983), have treated the diagnostic venation of extant auchenorrhynchan families. Since then, reassessments of older phylogenetic relationships, based on group diagnostics but not necessarily apomorphies, have been made for both the ancestral hemipteroid lineage (e.g., Kukalova-Peck & Brauckmann 1992), and for earlier hemipterans themselves (e.g., Shcherbakov 1984, 1988; Popov & Shcherbakov 1988, 1991). Figure 4 shows a current paleontological synopsis of euhemipteran lines.

These assessments suggest that the extant (monophyletic) Cicadomorpha (Clypeata sensu Shcherbakov) and Heteropterodea were derived from the Permian Prosboloidea [P_1-J_3] of the polyphyletic Cicadomorpha. Reputedly, the modern Cicadomorpha lineage evolved from an ancestor in the prosboloidean Prosbolidae

[P_2], along a lineage that involved Hylicellidae [T_3-K2] giving rise to: (a) Cicadoidea [T_3-R]; (b) Procercopidae [J_1-K_2], that begot Cercopoidea [J_1-R]; and (c) Karajassidae [J_{2-3}], that begot Cicadelloidea [J_2-R] (Shcherbakov 1988). A second prosbolid lineage begot Dysmorphoptilidae [P_2] (Shcherbakov 1984). A prosbolopseid Prosbolopseinae lineage gave rise to: (a) Palaeontinoidea [P_2-K_1]; and (b) Pereborioidea [P_2-T_3], the latter probably deriving Ignotalidae [P_2] (Shcherbakov 1984, 1988).

The Heteropterodea reputedly arose from a prosbolopseid Ingruidae [P_2] ancestor. The Coleorhyncha lineage began when ingruids begot Progonocimicinae [P_2-K_2], that begot Cicadocorinae [J_1-K_1] and Karabasiinae [J_1-K_2], the latter of which begot Hoploridiinae [K_1] and Peloridiidae [K?-R] (Popov & Shcherbakov 1991). The Heteroptera lineage reputedly arose when ingruids begot the Scytinopteroidae, the most primitive of which, Scytinopteridae [P_2-T_3], begot: (a) the Serpenivenidae [P_2-T_3] and their probable descendents, Stenoviciidae [P_2-T_3] and Paraknightiidae [T_3]; and later, (b) Ipsviciidae [J_{1-3}] (Shcherbakov 1984).

The origin of the Fulgoromorpha lineage is yet unclear. However, Shcherbakov (1984) suggests it arose from Archescytinoidea, independently of Cicadomorpha, towards the end of the early Permian. Assessment of Fulgoromorpha's Permian ancestors, reputedly Surijokocixidae [P_2-J_1] and Coleoscytoidea [P_{1-2}], is more tentative, and modern fulgoromorphan groups, such as Cixidae [K_1-R] and Achilidae [K_1-R], do not appear until the Cretaceous (Shcherbakov 1988), after the intervening presence of Fulgoridiidae [J] in the Jurassic (Bode 1953, Hamilton 1990, but see Wilson et al. 1994).

Thus, the paleontologically supported origin of Fulgoromorpha remains the most unsettling of the three major euhemipteran clades. Tracing early fulgoromorphans before the Jurassic is problematic because only tegmina occur then, but most fulgoromorphan apomorphies are head characters. The paleontological evidence, therefore, does not support clade Auchenorrhyncha, because of the polyphyletic nature of Cicadomorpha (sensu Shcherbakov). Presently, it would seem to most closely support the slightly less parsimonious 18S rDNA topologies that indicate clade modern Cicadomorpha+Heteroptera. In our opinion, however, the nucleotide-based topology is superior to very nebulous indications of origin for Fulgoromorpha that are revealed by fossils.

Eco-evolution of Hemipterans and Cladogenesis

What selective driving forces were responsible for the major cladogenic events that shaped the 18S rDNA topology of hemipterans? We believe that the divergence, establishment and success of major evolutionary lineages (as clades) requires the presence, recognition and exploitation of existing niches. At best, restrictive niches should hamper the evolutionary diversification of their exploitive tive lineages. New niches ("neoniches") that develop after the establishment of previously existing and non-competing clades, would permit multiple entry points for would-be competing invaders from multiple, existing clades. Such homoplasious invasions of any neoniche should require its delineation among the polyphyletic neocompetitors if all are to survive as neo(sub)clades of their respective parental clades. In time, each neoclade should genetically and morphologically differentiate from its parental clade, both before (cladogenic) and during (anagenic) its radiation in the neoniche.

Resultant convergence among the polyphyletic neoniche invaders would be dictated by niche-required morphology and function or other underlaying biological constraints (Wake & Larson 1987, Wake 1991). Neoniche radiations should be recognizable by the phylogenetic distributions of their taxa among parental clades whose basal section taxa have differing niche habitations. The eco-evolutionary constraints on such a scenario are the relative chronological developments of niches versus clades, the existence and degree of preadaptation or adaptive constraints (Moran 1988, 1990; Wake 1991), and potentially overlaying and inhibiting biogeographic demarcations.

The Hemiptera illustrate these tenets, and their early cladogenesis overlays the evolution of vascularization within plants. Clade Sternorrhyncha has *inter*cellular stylet-penetration of plants. Its most basal group, Psyllidae (Campbell et al. 1994), ingest from a variety of vascular and non-vascular tissues (Ullman & McLean 1988a, b). The Psyllidae's more derived sister-clade, Aleyrodiformes (Aphidoidea + Coccoidea + Aleyrodoidea, sensu Campbell et al. 1994), ingests predominantly when their stylet tips are within phloem sieve elements (Backus 1988, Janssen et al. 1989). In contrast, within clade Euhemiptera, Cicadomorpha and Fulgoromorpha have *intra*cellular stylet-penetration, with less precision than sternorrhynchans (Backus 1988). Clade Cicadomorpha initially evolved to feed on xylem (Cercopidae, Cicadidae, Cicadellidae: Cidadellinae), but has radiated to phloem (Membracidae, Cicadellidae: Deltocephalinae) and parenchyma (Cicadellidae: Typhlocybinae) as neoniches, presumably after the development of these plant tissues.

Both Sternorrhyncha and Cicadomorpha have developed varying types of filter chambers that are presumably used for osmoregulating profuse amounts of ingested hypotonic plant fluids. The sternorrhynchan filter (Evans 1963: type A) is simple and anteriorly expanded; the cicadomorphan filter (Evans 1963: type B) is complex and posteriorly expanded in association with the Malpighian tubules (Pesson 1944, Goodchild 1966). The relatively simple sternorrhychan filter was evolved by the appearance of the psyllids, who feed on various tissues, and was retained (probably parsimoniously) in their phloem feeding sister-clade Aleyrodiformes. Interestingly, psyllids are the only Sternorrhyncha that have retained all four Malpighian tubules; Aleyrodiformes have a reduced number or none (some aphids). The complexity of the cicadomorphan filter was probably required for xylem feeding, because that food source is very dilute; it also was retained (again, probably parsimoniously) among the cicadomorphan neoniche invaders (i.e., Membracidae, Cicadellidae: Deltocephalinae). All euhemipterans have retained all four Malpighian tubules.

It seems probable that early fulgoromorphans initially evolved to feed on roots and fungal hyphae, which exist in subterranean/semisubterranean (duff) niches, much as many of their immatures do now (Wilson et al. 1994). This selection probably happened because Sternorrhyncha and early Cicadomorpha (i.e., Cicadidae, Cercopidae, Cicadellidae: Cicadellinae), respectively, already had occupied intracellular and intercellular/xylem feeding niches, (before their secondary radiations onto later neoniches). Later, with the advent of phloem, fulgoromorphans probably moved readily into that neoniche and radiated. The Fulgoromorpha, lacking the filter chambers of the coexisting clades, probably found fine roots and fungal hyphae had relatively nutritious cells that are easily attacked; as

a food source, both these and phloem are less dilute than liquids from xylem. As a result, fulgoromorphans did not require development of an extraordinarily enlarged feeding pump, the associated, enlarged clypeal housing, or the specialized gut filter, that cicadomorphans did to handle the increased fluid load necessary for xylem feeding.

As cladogenesis of hemipterans progressed, and earlier ("homopteran") clades dominated both intra- and intercellular niches in developing vascular plant systems, their roots and soil fungi, the coleorhynchans appeared; their surviving relictual group, peloridiids, ended up on mosses, a nonvascular plant resource that was unoccupied by the other hemipteran clades. Probably because that niche is not diverse, coleorhynchans did not flourish, expand and radiate as did the sternorrhynchans, cicadomorphans and fulgoromorphans. However, their beginning gular development (Hamilton 1981: fig. 23), or rather that of their immediate ancestor in common with the heteropterans, began a change toward a prognathous rostrum and its liberating evolutionary potential.

In contrast to the Coleorhyncha, their sister-group, Heteroptera, evolved an alternative strategy, predation, which required the major and radical morphological shifts witnessed in the Enicocephalomorpha (Grimaldi et al. 1993). Once the predatory phena was accomplished, however, it opened vast new niches and environs for suctoral feeding on animalian body fluids, which up until then only mandibulate predators exploited. Predation as primary feeding strategy was exploited by most early heteropteran clades (Carver et al. 1991), and cladogenic radiation (Fig. 5) occurred in both terrestrial (Enicocephalomorpha, Dipsocoromorpha, Cimicomorpha), and aquatic/semiaquatic environs (Gerromorpha, Neomorpha, Leptopodomorpha). Although some groups among the more derived heteropteran clades reverted secondarily to phytophagy, they feed on parenchyma, seeds and pollen (Carver et al. 1991), which are largely unexploited by the "homopteran" clades. Only the Pentatomomorpha, a terminal heteropteran clade (Fig. 5) shows a major reversion to phytophagy. Wheeler et al. (1993) discuss the phylogenetic topology of Heteroptera, and Carver et al. (1991) discuss their biology.

Our 18S rDNA findings, in conjunction with other evidence for placement of the Coleorhyncha (Schlee 1969: 23, Popov & Shcherbakov 1991: 233, Wheeler et al. 1993: 131–132), suggests the preceding order of hemipteran cladogenesis. Available evidence indicates the major clades diverged by the late Permian, and scant synapomorphies linking these clades suggest rapid divergence of morphological form occurred. Frequent homoplasy within these developing clades probably resulted from evolutionary constraints (Wake & Larson 1987, Wake 1991). In conjunction with a relatively steady speed base substitution clock, the relatively few 18S rDNA synapomorphies shown among these clades (Fig. 3) functionally also indicates a relatively short time was involved during the cladogenesis. A similar 28S rRNA topology has been found for sponges, with deep radiations among clades that are separated by short internodes (Lafay et al. 1992).

Thus, a saltational and punctuated equilibrium mode of evolution appears to be involved among the basal hemipteran clades, and we suspect this may have resulted from sudden and dramatic selection pressures during the Permian, probably following one or more catastrophic truncation events. Ecomorphotypic diversity among every existing major group of vascular plants declined dramatically
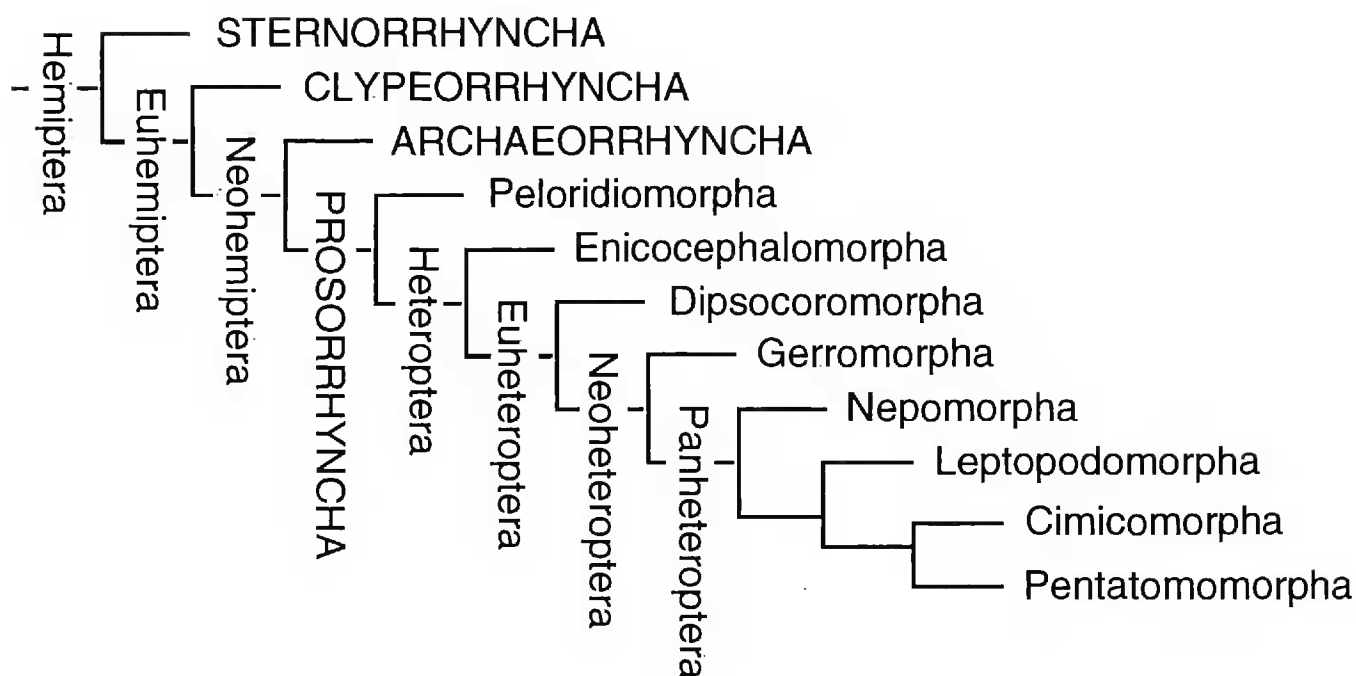
Figure 5. Phylogenetic relationships of proposed hemipteran suborders and existing (heteropterodean) infraorders. Horizontals depict the three basal clade suborders (capitals; Clypeorrhyncha = extant Cicadomorpha; Archaeorrhyncha = Fulgoromorpha) and the more derived infraorders (lower case; Peloridiomorpha = Coleorhyncha). Verticals depict the clade names (sensu Schuh 1979; lower case) and the proposed suborder Prosorrhyncha (capitals; = Heteropterodea, sensu Schuh 1979, as Coleorrhyncha + Heteroptera).

during the Permian (Shear 1991: 288), but rose again among the new angiosperms during the Cretaceous. This temporally changing aspect of plant diversity parallels the initiation of the major hemipteran clades (Permian) and their later internal radiation (late Jurassic/Cretaceous) into modern groups.

IMPLICATIONS FOR SUBORDER NOMENCLATURE

If our 18S rDNA-based topologies are correct, the paraphyly of Auchenorrhyncha requires its abandonment as a cladistic subordinal taxon of Hemiptera. Instead, recognition of four major hemipteran clades (sternorrhynchans, extant cicadomorphans, fulgoromorphans, heteropterodeans) as suborders is clearly appropriate (Fig. 5). We rely on the 18S rDNA synapomorphies of Wheeler et al. (1993), the morphological synapomorphies of Schlee (1969), and the fossil lineage assessment of Popov & Shcherbakov (1991: 233, as Coleorhyncha ← Ingruidae → Scytinopteroidea → Heteroptera) for placement of the Coleorhyncha as sister-clade to Heteroptera[8]. Despite anyone's lingering uncertainty concerning the relative phylogenetic topology among the major clades, there can be no doubt of their individual monophyly. Thus, demarcation of Hemiptera into these four major clades, as suborders, is a conservative treatment that preserves their morphological and ecological delineation.

Three new suborder names are proposed here, however, because several potential obfuscations confuse the application of the currently available names. First, there is a polyphyletic, paleontological use (e.g., Shcherbakov 1984) of Cicadomorpha, that differs from the one that is monophyletic covering extant taxa only (e.g., Carver et al. 1991). Second, there are varying definitions of Heteroptera, which may (e.g., Carver et al. 1991) or may not (e.g., Henry & Froeschner 1988)

[8] Recent molecular evidence based on 18S rDNA sequences (ex Wheeler et al. 1993) shows resolute synapomorphic sites supporting Coleorhyncha + Heteroptera monophylly; to be discussed elsewhere (Campbell et al., unpublished data).

include Coleorhyncha, versus Heteropterodea (e.g., Schuh 1979, Wheeler et al. 1993) or its alternative, initial spelling Heteropteroidea (Schlee 1969). Third, a problem exists regarding the implied relative hierarchical status of Cicadomorpha and Fulgoromorpha in contrast to heteropteran infraorders, which also end in suffix "-morpha" (e.g., Schuh 1979).

Standardizing on suffix "-rrhyncha" to denote suborder, we retain Sternorrhyncha, and propose as hemipteran suborders: (a) Clypeorrhyncha [Gr. "shield-nose"], for the monophyletic extant cicadomorphan taxa, (b) Archaeorrhyncha [Gr. "ancient-nose"], for Fulgoromorpha, and (c) Prosorrhyncha [Gr. "front-" or "forward-nose"], for clade Coleorhyncha+Heteroptera. We believe these names provide a much needed alleviation of confusion over the boundaries, hierarchical status and monophyly of these groups. Their application toward that end is feasible because the ICZN code does not require priority-basis recognition of subordinal names. In view of our 18S rDNA findings, the clade name Neohemiptera is also proposed for the clade Fulgoromorpha+Heteropterodea in Schuh's (1979) system (our clade Archaeorrhyncha+Prosorrhyncha).

It is appropriate, under this system, to refer to Coleorhyncha as Peloridiomorpha, indicating its infraordinal level within suborder Prosorrhyncha. Continued use of Coleorhyncha would imply its subordinal status, and necessarily that of Heteroptera, negating Prosorrhyncha. In contrast, use of Heteroptera can imply a greater clade division within suborder Prosorrhyncha (i.e., Hemiptera: Prosorrhyncha: Heteroptera), as the sister-group to Peloridiomorpha. Continued use of Fulgoromorpha and Cicadomorpha, however, would confuse their infra- and subordinal status. Moreover, use of Cicadomorpha confuses its paleontological versus extant taxonomic meaning; therefore, any such use should be in a non-cladistic fashion only, to indicate the extinct, polyphyletic Mesozoic taxa that may be relatives of the modern, monophyletic Clypeorrhyncha, but that lack all the latter's defining synapomorphies.

The logic for continuation of "-morpha" suffixed infraorders, and proposed adoption of "-rrhyncha" suffixed suborders, for Hemiptera is independent of, but related to, another question that should be asked. Because Hemiptera is monophyletic, and heteropterists generally use Heteroptera for "their group," perhaps it is time to recognize and address a common, often expressed resentment by many "homopterists," for whatever rationale, towards incorporation of those groups under the name Hemiptera. Unfortunately, Fabricius' (1775) neutral ordinal name, Ryngota, later modified to Rhyngota (Fabricius 1803) and then Rhynchota (Burmeister 1835), the latter championed by Hamilton (1981, 1983) and others (e.g., Dworakowska 1988), has been largely ignored for hemipterans. Adoption of Rhynchota may be appropriate as an admittedly political, but pragmatic, attempt at appeasing and unifying all "hemipterists" under one ordinal banner.

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Note added in final galley: The homoplasy (in literature) of sites 79 (dipterans, ex Carmean et al. 1992) and 454 (various heteropteran lineages, ex Wheeler et al. 1993) was discovered after acceptance of this manuscript, and was addressed in initial galley, along with insertion of footnotes 7 (p. 41) and 8 (p. 54). We have since tested the effect of removal of these sites on generation of the most parsimonious topology for the modified SET 4 matrix. The absence of 454, leaving only 19 nucleotides, created six MLTs (TL 28, CI 0.714) rather that the single SET 4 MLT. The additional absence of 79, leaving 18 nucleotides, produced the identical six topologies (TL 27, CI 0.704). These are:

(A) { { { { { CICAD , MIRID }, CERCO }, MEMBR }, DELPH }, STERN }
(B) { { { { { CICAD , MIRID }, MEMBR }, CERCO }, DELPH }, STERN }
(C) { { { { CICAD , MIRID }, { MEMBR , CERCO } }, DELPH }, STERN }
(D) { { { { { MEMBR , MIRID }, CERCO }, CICAD }, DELPH }, STERN }
(E) { { { { { CICAD , CERCO }, MEMBR }, MIRID }, DELPH }, STERN }
(F) { { { MEMBR , CERCO }, CICAD }, { DELPH , MIRID } } , STERN }

These MLTs all negate clade Auchenorrhyncha. MLT F is identical with the original SET 4 MLT, espousing clade Neohemiptera. MLT E places Heteroptera as sister clade to clade Clypeorrhyncha. MLTs A-C negate clade Clypeorrhyncha, placing the heteropteran variously among its members. The 50% majority rule consensus tree, with compatible groupings, from these MLTs is the same as MLT C, as:

{ { { { CICAD , MIRID } 50, { MEMBR , CERCO } 33 } 83, DELPH } 100, STERN }

However, our further analyses (see footnote 7) using additional taxa (Campbell et al., unpublished data), to be published elsewhere, together with significant morphological synapomorphies that we do not consider to be selection-induced homoplasies, indicate the monophylly of Clypeorrhyncha. Thus, our suborder proposal remains unaffected.